Herpetologica, 59(4), 2003, 469–474

PREY-HANDLING BEHAVIOR OF HATCHLING *ELAPHE HELENA* (COLUBRIDAE)

RITA S. MEHTA[1,2]

Department of Biology, University of Texas, Tyler, TX 75719, USA

ABSTRACT: The effects of prey size on prey-handling behavior for 60 ingestively naive hatchling *Elaphe helena* were studied in the laboratory. Hatchlings were randomly assigned to one of three diet categories in which prey (*Mus musculus*) varied by relative mass differences of 20–35%, 40–46%, or 50–59% of an individual snake's own body mass. The effects of prey size on capture position, direction of ingestion, condition of prey at ingestion (dead/alive), feeding duration, and prey-handling tactic were observed and recorded for each feeding episode. Results indicated that prey size significantly affected the prey-handling behavior of hatchling *E. helena*. In the largest relative mass category, hatchlings captured prey by the anterior end more often than in the smaller two relative mass categories. Prey from the smallest relative mass category were simply seized whereas, in the medium and large categories, pinion and constriction behaviors were observed. Time to subdue and ingest the prey item increased with prey size categories.

Key words: Colubridae; Effects of prey size; *Elaphe helena*; Prey-handling behavior

THE SIZE, type, and activity level of various prey are thought to influence the feeding behaviors for many advanced snakes (de Queiroz, 1984; Moon, 2000). Variation in feeding response to variables, such as prey size, are considered adaptive (Diefenbach and Emslie, 1971; Loop and Bailey, 1972; Sazima, 1989). Prey size may affect two aspects of the feeding repertoire: prey-handling and direction of ingestion. Many derived snakes simply seize small prey items and consume them alive, while larger prey items are pinned or constricted and killed prior to ingestion (Loop and Bailey, 1972). Loop and Bailey (1972) asserted that, independent of their phylogenetic position, snakes tend to swallow large endothermic prey head first. One hypothesis for this behavior is that head-first ingestion may reduce overall feeding time and that such a reduction in feeding time may be advantageous by allowing more time for other activities (de Queiroz and de Queiroz, 1987).

Independent of prey size, prey activity level can also affect prey-handling behavior. De Queiroz (1984) used gopher snakes (*Pituophis melanoleucus*) to show that a small, highly active prey item elicits a different feeding response than larger, inactive prey. Gopher snakes were significantly more likely to pinion (i.e., press prey against the substrate with the anterior portion of the body) and constrict small active mice than nestling rats. Furthermore, adult mice were more likely to be killed prior to ingestion than neonate rats. Gopher snakes were, thus, able to match their prey-handling behaviors to the activity level of their prey. A more recent electromyography study revealed that muscular activity and constriction pressure in gopher snakes changed in response to struggling of prey (Moon, 2000).

Most studies on snake feeding behavior are based on observations of adults, and knowledge of neonatal behavior is limited to a few studies (Mori, 1993*a*,*b*, 1994, 1995). Few studies address innate prey-handling behaviors for snake taxa that exhibit diversity in habitat, geography, and diet. In my study, I quantify the feeding behavior of hatchling *Elaphe helena*. This species is easy to maintain in a laboratory setting and data on prey-handling behavior exists for closely related species within the genus, allowing valuable comparisons. Adults of this species are recorded as preying on mammals but have also been known to incorporate lizards into their diet (Daniel, 1983). Whether or not hatchling *E. helena* undergo an ontogenetic shift in diet is unknown, as both mice and frogs have been found in wild-caught juveniles (Schulz, 1996). I also compare the feeding behaviors of *E. quadrivirgata*, *E. climacophora*, *E. taeniura*, and *E. dione* from the investigations of Mori

[1] PRESENT ADDRESS: Department of Psychology, University of Tennessee, Knoxville, TN 37996-0900, USA.
[2] CORRESPONDENCE: e-mail, rmehta2@utk.edu

(1991, 1993*a*,*b*) and Mori and Moriguchi (1988) to the feeding behavior of *E. helena*.

My study addresses the following four questions. What prey-handling behaviors are employed by hatchling *E. helena*? Do hatchling *E. helena* show a preference for head-first ingestion of prey? Do hatchling *E. helena* change prey-handling behavior according to prey size? How does the feeding behavior of *E. helena* compare to other Asian *Elaphe* species?

Materials and Methods

Experimental Procedures

I used 60 hatchling *E. helena* from seven different clutches. These clutches were laid January–May 2000 by four laboratory-raised females originally collected in Sri Lanka. Hatchlings averaged 32.61 cm ± SE 4.83 snout–vent length (SVL) and weighed 10 g ± SE 3.24 after their primary ecdysis. Hatchlings were housed in 3.8-l glass jars (diameter, 12.5 cm; height, 23 cm) and were kept at an ambient temperature of 25 C. Fluorescent lighting as well as sunlight provided illumination during the day. Each jar contained aspen bedding (2 cm deep) and a small water dish. Feeding tests were conducted over a period of 3 mo when snakes were 15–30 d old. All study subjects were ingestively naïve when trials commenced. Hatchlings were randomly assigned to one of three prey-size groups (small, medium, and large). Each group contained 20 snakes. Prey size relative to snake size was expressed as a mass ratio (MR = prey mass/predator mass; Gans, 1961; Greene, 1983). Small prey ranged from 20–35% of the body mass (BM) of the hatchling. Medium and large prey comprised 40–46% and 50–59%, respectively, of the BM of the hatchling. Each hatchling was only tested once.

Feeding trials took place at 1800–2100 h. One hour prior to the experiment, an individual was placed in a 20-l terrarium lined with a sheet of white butcher paper and left to habituate to the enclosure. A red light was used to illuminate the experimental arena. Each trial began with the introduction of a single, live, newborn mouse (*Mus musculus*) of the appropriate size class into the terrarium using a pair of 50-cm forceps. All feeding behaviors of the snakes were observed as well as recorded with an 8-mm Sharp video recorder VL-E43U until the mouse was completely swallowed. If the snake did not attack the mouse within 45 min, the trial was terminated and repeated 3 d later. I followed eight variables during each trial (Table 1).

The MR categories served as independent variables, and the behaviors in each category represented dependent variables. The effects of relative prey size on aspects of feeding duration were assessed with ANOVA and Tukey's (HSD) tests. Non-parametric multiple comparisons were used to examine prey-handling behavior in which Kruskall-Wallis tests were used for more than two samples. Binomial tests were used to assess whether head-first or tail-first ingestion was more common. The level of significance of all tests was $P \leq 0.05$.

Results

Twelve of 60 hatchlings refused to eat on the first trial, but eventually all hatchlings of *E. helena* fed during the experimental period. All 60 individuals were used in the following analysis. There were significant differences in capture positions among relative prey weights ($F_{(2,57)} = 5.769$, $P = 0.015$). Post hoc pairwise comparisons indicated differences between the small and large MR categories ($F_{(1,57)} = 16.44$, $P < 0.05$). Mice tended to be captured head first as prey increased in size. Prey items were not captured by the middle part of the body.

Seven prey-handling behaviors were observed during feeding trials. The methods employed were simple seizing (SS), delayed pinion (DP), delayed hairpin loop (DHL), delayed constriction (DC), immediate pinion (IP), immediate hairpin loop (IHL), and immediate constriction (IC). Different sets of these prey-handling behaviors emerged as MR increased. A Kruskal-Wallis test revealed a difference in the overall frequencies of the prominently seen prey-handling behaviors (SS, IHL, IC) with respect to each of the three MR categories (SS: $H = 11.784$, df = 2,57, $P = 0.003$; IHL: $H = 8.429$, df = 2,57, $P = 0.015$; IC: $H = 15.602$, df = 2,57, $P < 0.005$). Simple-seizing was most frequent in the small and medium MR categories, while IC was only observed in the large MR category

TABLE 1.—Behaviors recorded during snake-prey encounters (after Mori, 1991, 1994).

Behavior	Definition
Capture position	Part of the prey's body first grasped by the hatchling: anterior (head and shoulder), middle (abdomen and forelegs), or posterior (pelvic region, hind legs, and tail)
Prey-handling method	Simple seizing (SS): grasping the prey in its jaws without subduing it with the body; pinion (P): pressing the prey against the substrate by the snake's body; hairpin loop (HL): squeezing the prey between non-overlapping portions of the snake's body; constriction (C): constricting the prey by a fully encircling loop. Each of these behaviors can be performed immediately (I) after capture or delayed (D) 1 or more seconds after prey capture
Condition of prey before ingestion	Dead or alive
Effectiveness of constriction	Evaluated only when the snake exhibited immediate coiling (HL, C). Four criteria were used: (1) Result of immediate coiling: the snake successfully coiled around the prey (success) or the snake attempted to coil the prey by typical wrapping and/or winding movements (Greenwald, 1978) but was unsuccessful (fail) (2) Coil release: after successful immediate coiling the snake released its coil within 10 s after striking because of irregular, unstable coiling and/or struggling of the prey (coil release) (3) Occurrence of re-constriction: the snake attempted to re-constrict after initial failure (4) Overall number of prey items killed via constriction
Swallowing position	Anterior or posterior end of prey first
Time to subdue prey	Time from the moment the prey was struck or seized to the start of swallowing
Time to ingest prey	Time from the start of swallowing to the point at which the snake began pushing the prey toward its midbody and the snake's mouth could completely close
Feeding duration	Time from prey capture to prey ingestion as timed and recorded

(multiple comparisons; Fig. 1). The prey-handling behaviors observed the least across all relative mass categories were DHL and DC.

There were significant size differences between mice killed and mice swallowed alive ($F_{(2,57)} = 10.813$, $P < 0.01$). Mice were killed before ingestion only in the largest MR category and then in only 25% of large prey encounters. In the large prey category, IC was the single method used to subdue as well as kill mice. Eight individuals successfully coiled around their prey after the initial attack. Of these eight individuals, five killed their prey before ingestion. Six different individuals released their coils within 10 s of striking prey because of unstable coiling. All six of these individuals were observed re-constricting their prey.

Among the three MR categories, there were significant differences in prey size between mice swallowed head first and tail first (Fig. 2; Z = 6.043, df = 2,57, $P = 0.017$). The number of snakes ingesting prey head first was positively related to relative prey mass. Tail-first ingestion was the preferred direction for the smallest MR category.

The mean time to subdue prey differed significantly among the three MR categories ($F_{(2,57)} = 54.42$, $P = 0.034$; Fig. 3). Significant differences resulted between the small and medium MR ($F_{(1,58)} = 60.84$, $P = 0.013$) and medium and large MR ($F_{(1,58)} = 53.22$, $P = 0.042$). Mean time to ingest prey differed significantly between the prey MRs ($F_{(2,57)} = 43.48$, $P < 0.01$). Post hoc tests revealed significance between the small MR category and the medium MR category ($F_{(1,58)} = 77.14$, $P < 0.001$) and the medium and large MR ($F_{(1,58)} = 79.22$, $P < 0.001$). Total feeding duration significantly varied between the three groups ($F_{(2,57)} = 57.315$, $P = 0.017$). Differences in total feeding duration were significant between the small and medium MR ($F_{(1,58)} =$

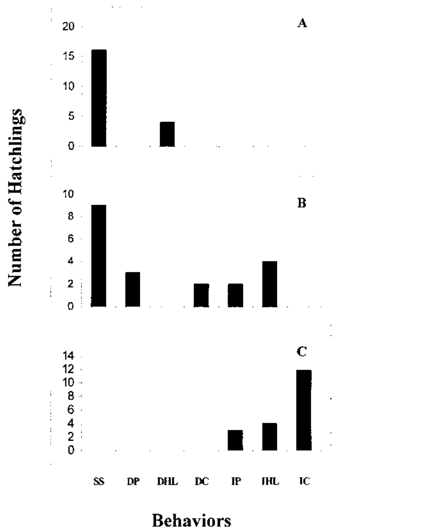

FIG. 1.—Number of hatchlings of *Elaphe helena* exhibiting the following seven prey-handling behaviors in three relative prey mass ratio categories: (A) 20–35%; (B) 40–46%; and (C) 50–59%. Each category contained 20 hatchlings and exhibited the following behaviors: simple-seizing (SS), delayed pinion (DP), delayed hairpin loop (DHL), delayed constriction (DC), immediate pinion (IP), immediate hairpin loop (IHL), and immediate constriction (IC).

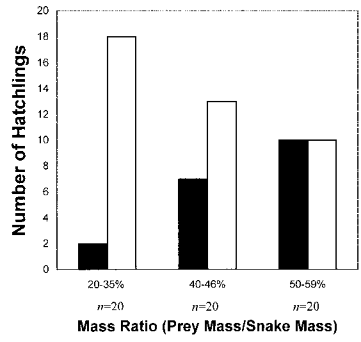

FIG. 2.—Observations of direction of ingestion for hatchlings of *Elaphe helena* in the three mass ratio categories (20–35%, 40–46%, and 50–59%). Each weight class contained 20 hatchlings. White bars represent tail-first ingestion and black bars indicate head-first ingestion.

66.23, $P < 0.001$) and medium and large MR ($F_{(1,58)} = 58.80$, $P < 0.003$). The greatest difference in total feeding duration was evident between the small and large MR categories ($F_{(1,58)} = 76.80$, $P < 0.001$).

DISCUSSION

Feeding behavior for hatchlings of *E. helena* varied with prey size. As prey MR increased, the frequency of hatchlings capturing prey by the head also increased. Seven handling methods were observed during the experimental period, and, within each MR category, a particular prey-handling mode dominated (Fig. 1). These results suggest that hatchlings of *E. helena* are able to employ different handling behaviors when presented with different prey-size-specific stimuli. Hatchlings coiled larger prey items, while, for smaller prey items perhaps perceived as less challenging, they simply seized and swallowed the prey alive.

Direction of ingestion for ingestively naive *E. helena* differed between the different MR categories. The occurrence of head-first ingestion did not significantly increase as food items increased in MR, suggesting that head-first ingestion of prey for hatchlings of *E. helena* might not be an innate behavior, at least when consuming endothermic prey. Tail-first ingestion was actually the predominant direction of ingestion for the 20–35% and 40–46% MR categories. In the largest MR category, equal numbers of prey were consumed head first as were consumed tail first. The stimuli mediating discrimination of the head remain unclear and could vary with taxa. Some snakes may learn to ingest prey by trial and error, while other snakes may have an innate response (Greene, 1997). Hatchling rat snakes and king snakes may use cues, such as

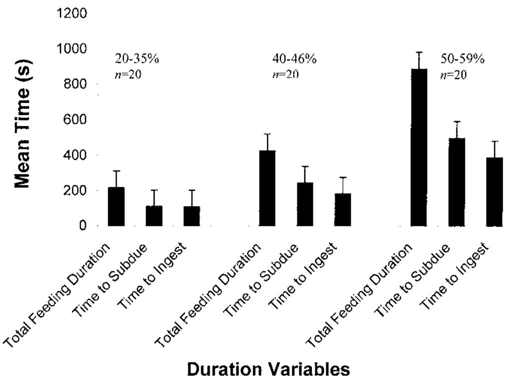

FIG. 3.—Comparison of the means for time to subdue, time to ingest, and total feeding duration for the three mass ratio categories (20–35%, 40–46%, and 50–59%) in hatchlings of *Elaphe helena*. Each category contained 20 hatchlings.

the direction of hair or scales, the shape of the snout, and the texture of the underlying skull, to guide direction of prey ingestion (Greene, 1997).

The interval between prey capture and prey ingestion (time to subdue prey) varied dramatically between the different MRs as well as between the different methods used to subdue the prey item. The most time intensive part of prey handling was the time required to subdue the prey item; this probably reflects the lack of experience by hatchling snakes. A study of ontogenetic mechanisms in prey-handling behavior of *E. helena* is needed to determine if head-first ingestion and efficiency in handling prey increases with experience, as well as whether tail-first ingestion actually does increase swallowing time.

Subduing prey by hatchlings of *E. helena* entailed pinning the prey item and more or less constraining the prey rather than killing it, much like behaviors observed in adult *Thamnophis elegans* (de Queiroz and Groen, 2001; Gregory et al., 1980). Only in the largest MR category, where hatchlings ingested 50–59% of their own mass, was prey killed before ingestion. Prey in the largest mass category was killed by constriction, and the duration to subdue the prey was considerably increased. This increase in time to subdue larger prey and the fact that only 25% of large prey was killed by constriction may indicate that hatchlings of *E. helena* are not effective constrictors, or at least during the first encounter with endothermic prey. Very few individuals were able to use constriction as a means of subduing and killing the prey item. Also, some individuals uncoiled while struggling with prey. Lack of effectiveness may be due to immaturity of the muscles that are used for constricting. Hatchlings that were successful in killing prey via constriction, however, were not significantly bigger than the other hatchlings within the same MR category or between MR categories.

The prey-handling behavior of *E. helena* is unique in the sense that coils were applied by winding with the posterior body without an initial twist. The coil behavior for other species of *Elaphe* is described as winding with the anterior body without an initial twist (Greene, 1977; Mori, 1991; Steward, 1971). On three different occasions when *E. helena* were accidentally disturbed while coiling around a prey item, the hatchlings were able to go into a defensive posture with the anterior portion of their body while the posterior portion was still wrapped around the prey. Coiling around the prey with the posterior portion of the body may be a way that hatchlings can maintain defensive vigilance while feeding. However, it is possible that coiling with the posterior portion of the body is due to inexperience with the prey item as well as a lack of muscle maturity.

Three hypotheses, not mutually exclusive, have been proposed for the different responses to various sized prey items observed in some colubroids (Mori, 1991): (1) reduction of total prey-handling time, (2) protection of the snake itself from retaliation, such as biting, by the attacked prey, and (3) prevention of escape by the captured prey. My study indicates that prey size affects the predatory behavior of *E. helena*. Small prey items were simply seized, and larger prey items elicited the behaviors of pinion and constriction. In my study, the possibility of retaliation by mice in any of the three MR categories was unlikely since mice were still in an altricial state. For the same reason, escape by the captured prey was not possible. Hatchling snakes are probably using both tactile cues and the actual weight of the prey as indicators of which prey-handling behaviors to adopt. Ultimately, these varied responses to prey of different size may enable these snakes to minimize prey-handling time.

My results are consistent with the findings of Mori (1994) and further demonstrate the diversity of responses to prey size in Old World *Elaphe*. The proficiency of constriction by hatchlings of *E. helena* is intermediate to that of good constrictors such as *E. climacophora* and poor constrictors such as *E. quadrivirgata*. My study further substantiates that there is a certain degree of variation in hatchling feeding behavior, even within the same genus. Young, inexperienced animals may reveal that specialized motor patterns exhibited in adults have distinct developmental histories in different taxa (Burghardt, 1978, 1993). Differences in the development of certain motor patterns may be linked to other behaviors, such as defensive postures. Species of the genus *Elaphe* (sensu lato) exhibit a variety of prey-handling behaviors that may be associated with their diverse ecologies. Future studies examining geographic variation and maternal effects on prey-handling behavior in colubrids may reveal extensive plasticity in feeding behavior of advanced snakes.

Acknowledgments.—I thank L. Almli, G. M. Burghardt, P. A. Burrows, L. Ford, N. B. Ford, R. Gutberlet, M. Kearney, J. Manrod, A. Mori, J. S. Placyk, Jr., J. T. Redwine, and R. Reiserer for helpful suggestions on this manuscript. Animals were kept in captivity in accordance with the University of Texas at Tyler Animal Care Protocol. This project was completed in partial fulfillment of the MS degree from the University of Texas at Tyler under the supervision of N. B. Ford.

Literature Cited

Burghardt, G. M. 1978. Behavioral ontogeny in reptiles: whence, whither, and why? Pp. 149–174. *In* G. M. Burghardt and M. Bekoff (Eds.), The Development of Behavior. Garland, New York, New York, U.S.A.

———. 1993. Comparative imperative: genetics and ontogeny of chemoreceptive prey responses in natricine snakes. Brain, Behavior and Evolution 41:138–146.

Daniel, J. C. 1983. The Book of Indian Reptiles. Bombay Natural History Society, Leo at St. Francis Industrial and Technical Institute, Borivli, Bombay.

de Queiroz, A. 1984. Effects of prey type on the prey-handling behavior of the bull snake, *Pituophis melanoleucus*. Journal of Herpetology 18:333–336.

de Queiroz, A., and K. de Queiroz. 1987. Prey-handling behavior of *Eumeces gilberti* with comments on head first ingestion in squamates. Journal of Herpetology 21: 57–63.

de Queiroz, A., and R. R. Groen. 2001. The inconsistent and inefficient constricting behavior of Colorado western terrestrial garter snakes, *Thamnophis elegans*. Journal of Herpetology 35:450–460.

Diefenbach, C. O., and S. G. Emslie. 1971. Cues influencing the direction of prey ingestion of the Japanese rat snake, *Elaphe climacophora* (Colubridae, Serpentes). Herpetologica 27:461–466.

Gans, C. 1961. The feeding mechanisms of snakes and its possible evolution. American Zoologist 1:217–227.

Greene, H. W. 1977. Phylogeny, convergence, and snake behavior. Ph.D. Dissertation, University of Tennessee, Knoxville, Tennessee, U.S.A.

———. 1983. Dietary origins and radiation of snakes. American Zoologist 23:431–441.

———. 1997. The Evolution of Mystery in Nature. University of California Press, Berkeley and Los Angeles, California, U.S.A.

Greenwald, O. E. 1978. Kinematics and time relations of prey capture by gopher snakes. Copeia 1978: 263–268.

Gregory, P. T., J. M. Macartney, and D. H. Rivard. 1980. Small mammal predation and prey-handling behavior by the garter snake, *Thamnophis elegans*. Herpetologica 36:87–93.

Loop, M. S., and L. G. Bailey. 1972. The effects of relative prey size on the ingestion behavior of rodent-eating snakes. Psychonomic Science 28:167–169.

Moon, B. R. 2000. The mechanics and muscular control of constriction in gopher snakes (*Pituophis melanoleucus*) and a king snake (*Lampropeltis getula*). Journal of Zoology (London) (2000) 252:83–98.

Mori, A. 1991. Effects of prey size and type on prey-handling behavior in *Elaphe quadrivirgata*. Journal of Herpetology 25:160–166.

———. 1993*a*. Does feeding experience with different size of prey influence the subsequent prey-handling behavior in *Elaphe climacophora*? Ethology 11:153–156.

———. 1993*b*. Prey handling behavior of neonatal rat snakes, *Elaphe taeniura* and *E. dione* (Colubridae). Japanese Journal of Herpetology 15:59–63.

———. 1994. Prey-handling behavior of newly hatched snakes in two species of the genus *Elaphe* with comparison to adult behavior. Ethology 97:198–214.

———. 1995. Prey handling behavior of the young rat snake *Elaphe taeniura* (Squamata: Reptilia). Kyoto University Series of Biology 16:43–47.

Mori, A., and H. Moriguchi. 1988. Food habits of the snakes in Japan: a critical review. Snake 20:98–113.

Sazima, I. 1989. Feeding behavior of the snail-eating snake, *Dipsas indica*. Journal of Herpetology 23:464–468.

Schulz, K. 1996. A Monograph of the Colubrid Snakes of the Genus *Elaphe* Fitzinger. Koeltz Scientific Books, Czech Republic.

Steward, J. W. 1971. The Snakes of Europe. Fairleigh Dickinson University Press, Canterbury, New Jersey, U.S.A.

Accepted: 15 May 2003
Associate Editor: Carl Anthony